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Dispersal and population connectivity are phenotype dependent in a marine metapopulation

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Larval dispersal is a key process determining population connectivity, metapopulation dynamics and community structure in benthic marine ecosystems, yet the biophysical complexity of dispersal is not well understood. In this study, we investigate the interaction between disperser phenotype and hydrodynamics on larval dispersal pathways, using a temperate reef fish species, Trachinops caudimaculatus. We assessed the influence of larval traits on depth distribution and dispersal outcomes by: (i) using 24-h depth-stratified ichthyoplankton sampling; (ii) quantifying individual phenotypes using larval growth histories extracted from the sagittal otoliths of individual larvae; and (iii) simulating potential dispersal outcomes based on the empirical distribution of larval phenotypes and an advanced biological-physical ocean model. We found T. caudimaculatus larvae were vertically stratified with respect to phenotype, with high-quality phenotypes found in the bottom two depth strata, and poor-quality phenotypes found primarily at the surface. Our model showed high- and average-quality larvae experienced significantly higher local retention (more than double) and self-recruitment, and travelled shorter distances relative to poor-quality larvae. As populations are only connected when dispersers survive long enough to reproduce, determining how larval phenotype influences dispersal outcomes will be important for improving our understanding of marine population connectivity and persistence.

1. Background

Metapopulations are networks of discrete populations distributed across fragmented landscapes, connected through the migration or dispersal of individuals [1] Dispersal—the movement of individuals or propagules across space—allo processes in ecology and evolution, from structuring local population demographics [3] to enabling adaptation and speciation [4]. Understanding the mechanisms that determine dispersal outcomes is therefore critical for predicting population connectivity and metapopulation dynamics, and the ability of a species to respond to environmental change [5,6].

Across many taxa and systems, growing evidence has suggested that dispersal is not random, and successful dispersers are often not a random draw from a population [5,7]. Instead, an individual's decision or ability to disperse depends on the interaction between its phenotype and its environment [8,9]. Furthermore, dispersal does not evolve independently of other traits; it has been shown to covary with suites of ecologically important phenotypic traits (e.g. morphological, physiological, behavioural and life-history)—creating disperser phenotypes, or predictable disperser syndromes both within and among species (e.g. [10,11]). This non-randomness in trait distribution across a population often results in strong phenotypic differences between individuals that disperse and those that stay [8,9].

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64 Dispersal syndromes have been examined extensively in 65 terrestrial ecosystems (e.g. [12,13]). However, in marine sys-66 tems, where dispersal during a species' pelagic larval stage 67 plays a critical role in connecting geographically separated 68 (i.e. benthic or demersal) adult populations (e.g. [14]), dispersal 69 syndromes have not been widely studied. In a marine context, 70 research has focused on how larval condition or phenotype can 71 influence success in subsequent life stages, with the fitness and 72 survival in the post-settlement environment strongly linked to 73 phenotypic traits of dispersers for many marine organisms 74 (e.g. size-at-hatch [15,16], larval growth (e.g. [17,18]), and over-75 all 'quality' of larvae at settlement [19]). Despite growing 76 research interest in phenotypic links across life stages in 77 marine systems, we have little knowledge of how phenotypic 78 traits of dispersers interact with their environment to influence 79 dispersal outcomes, or their ability or decision to disperse in 80 the first place.

81 In the open ocean, it is well known that many marine 82 larvae are capable of substantially modifying their horizontal 83 dispersal trajectory by altering their vertical position in the 84 water column (e.g. [20,21]). Due to differences in the strength 85 of ocean currents from the surface to the ocean floor, even 86 small differences in vertical position can have large effects on 87 the distance an individual can disperse [22]. It was first 88 suggested by Blaxter & Ehrlich [23] that larval condition 89 could influence an individual's vertical movement or posi-90 tioning in the water column, though this has never been 91 empirically tested.

92 In this study, we investigate the influence of disperser 93 phenotypes on larval dispersal pathways in a population 94 of southern hulafish (Trachinops caudimaculatus), a temperate 95 reef fish. Specifically, we assessed the influence of larval 96 traits, including size and growth attributes, on vertical distri-97 bution throughout the water column and dispersal outcomes 98 by (i) using 24-h depth-stratified ichthyoplankton sampl-99 ing to determine the depth distribution patterns of larval 100 T. caudimaculatus; (ii) quantifying individual phenotypes 101 using larval growth histories extracted from the sagittal 102 otoliths of individual larvae; and (iii) simulating dispersal outcomes based on the observed distribution of larval phenotypes 103 104 and an advanced biophysical larval dispersal model. We 105 hypothesized that larval phenotype will influence the position 106 of a larva in the water column, and ultimately influence the 107 dispersal outcome of the individual. Understanding the com-108 plex interactions between phenotypic traits and environment, 109 and the influence of disperser phenotypes on population 110 connectivity, is critical for developing effective conservation 111 strategies and for managing spatially structured marine 112 populations in a changing environment [8,14,16,24].

2. Methods

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(a) Study location and species

This study was conducted in Port Phillip Bay (PPB, surface area: 118 1930 km²; mean depth: 12.8 m) [25], a semi-enclosed embayment 119 on the southeast coast of Australia. Semi-diurnal tides dominate 120 the hydrodynamics of PPB, though tidal currents decrease with 121 distance from the ocean, peaking at 1 ms^{-1} at the Southern Ocean entrance and only 0.02 ms^{-1} in the north of the Bay [26]. 122 123 Vertical stratification of temperature and salinity in PPB is rela-124 tively rare, though vertical shear is always present, with 125 currents near the surface varying in magnitude and direction 126 to currents at middle or bottom depths [25].

Trachinops caudimaculatus is a small-bodied (less than 150 mm), short-lived (1-5 years) zooplanktivorous demersal fish found in high abundance on reefs throughout Southern Australia [27]. Throughout the study site of PPB, juvenile and adult populations of T. caudimaculatus inhabit discrete patches of rocky reef surrounded by soft sediment. Rocky reef in PPB is sparse and patchily distributed mainly along the coastal fringes (less than 8 m depth), comprising only 0.5% of the Bay [26]. As the most abundant reef fish in PPB, occupying 89% of the reefs in the shallow rocky reef system [28], T. caudimaculatus is an ideal model species for gathering empirical data on larval dispersal and consequences for population connectivity in this semi-enclosed system. Trachinops caudimaculatus hatch from demersal eggs, and once hatched, larvae remain in the plankton for 30-50 days before settling back to rocky reef habitat [28]. As adults are highly reef-attached, dispersal only occurs in the pelagic larval life stage.

(b) Sampling protocol

Depth-stratified sampling of T. caudimaculatus larvae was undertaken during the austral summers of 2012/13 and 2013/14 at Schnapper Point, Mornington (38°12' S, 145°01' E) on the southeastern coast of PPB. The location and depth (approx. 10 m bottom depth) of sampling was chosen based on proximity to one of the largest T. caudimaculatus populations in the Bay. The 24-h sampling events were initiated after T. caudimaculatus larvae were found during preliminary surveys, and continued through the T. caudimaculatus dispersal period. Ichthyoplankton samples were collected at four depth strata: surface (top 0-1 m of the water column), 3 m, 6 m, and bottom (approx. 10 m) using a 500 µm mesh plankton net with a circular mouth of 80 cmdiameter (surface and mid-water samples), and a 500 µm mesh benthic sled with a rectangular mouth ($60 \text{ cm} \times 125 \text{ cm}$; benthic samples). Ichthyoplankton samples were collected continuously Q1 for a 24-h period. See electronic supplementary material 1 for sampling dates and detailed sampling protocol.

In the laboratory, *T. caudimaculatus* larvae were identified and counted. Larval abundances were standardized to number of fish per 100 m³ based on flow-meter determinations of the volume of water filtered per tow.

(c) Vertical distribution patterns

To evaluate patterns of vertical distribution in relation to tides, diel cycle and date, the package 'glmmADMB' [29] was used in R, with function glmmadmb to fit a zero-inflated generalized linear mixed model (GLMM) to larval density. A negative binomial distribution was used to account for the detected over-dispersion. Depth (4 levels: 0 m (surface), 3 m, 6 m, 10 m (bottom)), tide (2 levels: ebb, flood), and time of day (3 levels: day, night, crepuscular periods) were included as fixed factors, and collection date as a random factor to account for variation in larval abundance resulting from seasonality in spawning. To test for the effects of the fixed factors on T. caudimaculatus larval density, a series of increasingly complex models were compared using Akaike Information Criterion for small sample sizes (AICc) for selection of the model of best fit. These values were rescaled as the difference between each model and the model with the lowest AIC_c (ΔAIC_c) to evaluate model performance, along with the Akaike weights for each model. This analysis was conducted in the statistical software R [30] using the packages 'AICcmodavg' [31] with function AICctab and 'MuMIn' [32]. We inferred statistical significance of the main effects that were included in the best-fit model, and assessed the strength of the retained parameter estimates through inference tests (Wald statistic, glmmADMB package).

(d) Quantifying larval quality

Otoliths were extracted from 291 *T. caudimaculatus* larvae, by randomly sub-sampling fish from each plankton sample

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(10 individuals per sample depth, block and collection date, or all
individuals if sample had less than 10). Details on otolith preparation and imaging can be found in electronic supplementary
material 1.

For each otolith, hatch checks were identified, generally charac-131 terized by an abrupt decrease in increment widths, which typically 132 coincided with a change in the optical density of the otolith. Larval 133 age based on number of post-hatch daily increments was also 134 recorded. Three phenotypic variables were estimated from the 135 daily increments formed during the pelagic larval stage, and 136 used to characterize individual larval phenotype: (i) size-at-137 hatch, estimated as the postrostral radius from the core to the 138 hatch check; (ii) early larval growth, estimated as the mean increment width across the first 5 days of larval growth following 139 hatching; and (iii) instantaneous larval growth rate (IGR), esti-140 mated from plotting individual otolith growth increments from 141 the dispersal period (post-hatch), and using the linear model 142 Lt = mt + b, where Lt is the otolith size (µm) at age t (day), b is the 143 otolith size at t = 0, and mt is the instantaneous growth rate (i.e. 144 the slope of the line of best fit, or the 'per µm, per day' rate of 145 increase). A linear growth model was used to determine IGR 146 because at such small larval sizes the growth relationship was 147 observed to be linear. These three measures of larval phenotype 148 provide complimentary information and were not independent 149 (size-at-hatch versus early larval growth: r = 0.30; p < 0.0001; sizeat-hatch versus IGR: r = 0.39; p < 0.0001; early larval growth 150 versus IGR: r = 0.74, p < 0.0001). Therefore, we used a principal 151 component analysis (PCA) to generate a composite measure of 152 larval phenotype, estimated as the first principal component 153 score (PC1 explained 66% of overall variation) for each fish [16]. 154 An underlying assumption of this analysis is that otolith growth 155 rate is correlated with somatic growth rate of the larva; for individ-156 uals in our study where otolith radius and larval standard length 157 (SL) data existed (n = 277), otolith size did correlate with SL 158 (Pearson's r = 0.86).

(e) Analysis of variation in larval quality

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As there was no evidence of vertical migration by T. caudimacula-162 tus larvae (see Results), a reduced model with greater relevance 163 to our research questions was used for all further analyses. To 164 evaluate whether phenotypic traits of T. caudimaculatus larvae 165 varied as a function of depth, we used the lme4 package [33] 166 in R to fit a linear mixed effects model with the first principal 167 component score resulting from a PCA on the three larval pheno-168 typic traits (described above) as the response variable, depth as a 169 fixed factor, and collection date as a random factor. In addition, 170 we used lme4 to fit a linear mixed effects model to larval age, 171 with depth as a fixed factor and collection date as a random 172 factor, to assess whether larval age varied as a function of depth. We used the same method to fit a linear mixed effects 173 model to larval otolith size at age, with depth as a fixed factor 174 and collection date as a random factor, to examine the growth 175 trajectories of larvae at different depths. P-values were obtained 176 by likelihood ratio tests of the full model with the effect in ques-177 tion against the model without the effect in question. Where full 178 models were significant, post hoc pairwise comparisons of signifi-179 cant terms were conducted using Tukey's honestly significant 180 difference (HSD) test, using the glht function in the 'multcomp' 181 package [34]. 182

(f) Dispersal model

A biophysical dispersal model was used to simulate potential dispersal outcomes based on the observed larval phenotypes [35]. The model uses a three-dimensional hydrodynamic model (400 m horizontal resolution, 8 vertical layers, and hourly time-steps [36]) of PPB, incorporating wind, sea level, temperature, air

pressure, tides, and solar radiation forcing [37], combined with high-resolution rocky reef habitat data for PPB [38] to represent the physical domain of the model. Detailed descriptions of the hydrodynamic model can be found in [39] and [40]. A particletracking model [35] was then used to simulate the dispersal and settlement of larvae throughout PPB, with empirically-derived biological and behavioural parameters (described in electronic supplementary material 2; table S1). Dispersal ensembles were completed for each suite of biological parameters matching known and hypothesized values for three different disperser phenotypes: (i) poor quality (i.e. small size at hatch, slow growing); (ii) average quality (i.e. large size at hatch, fast growing).

Within each ensemble, simulated larvae were released from 34 reef habitat patches around PPB (electronic supplementary material 2; figure S2); 1000 larvae were released within the bottom 5% of the water column, hourly from 19.00 to 01.00 daily from 1 October to 30 October 2009 (total of approx. 7.4 M larvae), a year for which we have a well-validated hydrodynamic model (e.g. [35]). The spawning window, location and timing of larval release were chosen to reflect reality, as T. caudimaculatus larvae typically spawn continuously (electronic supplementary material 2; figure S3) from late September to November immediately above the rocky reef substrate [28]. The maximum pelagic larval duration (PLD) was set for 50 days, after which any larvae that had not yet settled to a reef were considered dead. All individuals that survived the dispersal phase and reached competency had the capacity to sense and swim (at speed Sp) towards nearby habitat patches, at a given homing distance from reef habitat, and settle. The total settlement of larvae to all reef patches following spawning at each unique source was quantified. From these settlement patterns, the probability of movement between each set of reefs was calculated [35]. The migration matrix was derived by multiplying these settlement likelihoods with the source patch strength (i.e. reproductive output) to quantify the proportional settlement to each destination patch that came from each source population [35,41].

The three phenotype-based dispersal ensembles were integrated to create a migration matrix representing the mixed quality larval cohort and settlement patterns. Using the PC1 scores as a proxy for larval quality, we calculated the relative proportion of each phenotype within a dispersing larval cohort from each source patch. If larvae with a score less than –1 are considered 'poor quality' and those greater than 1 are considered 'high quality' then the following represents the proportion of each larval phenotype dispersing from a given patch: 23.4% low-quality larvae, 55.6% medium-quality and 21.0% high-quality larvae. These proportions where used to estimate the reproductive output of the three larval phenotypes from each source patch, in calculating the flow of individuals to destination patches. These three dispersal ensembles were then integrated to yield a migration matrix based on the mixed cohort settlement patterns.

The proportion of individuals that were released from a site and recruited back to their natal habitat patch, termed local retention (LR), and the proportion of all arriving individuals originating from the focal patch, or self-recruitment (SR), were calculated from the model output and the migration matrix. In addition, we quantified the mean relative geographical distance (GD) displaced by individuals, a distance-based measure of connectivity, and the proportion of individuals lost (PL) in the plankton (i.e. did not settle) from the model output. To assess whether these dispersal outcomes varied as a function of larval quality, we used the lme4 package in R to fit separate linear mixed effects models with mean LR, mean SR, mean GD, and PL as the response variables, larval quality as a fixed factor and reef ID as a random factor. Mean LR and mean SR was examined from both individual dispersal ensembles and from the integrated migration matrix. p-values were obtained by likelihood ratio tests of the full model with the

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19211 Table 1. Parameter estimates and test statistics for the selected model describing the distribution of *T. caudimaculatus* larval density as a function of depth. 191

parameter	estimate (s.e.)	z stat	<i>p</i> -value	-CI	+CI
depth					
intercept (surface)	1.246 (0.775)	1.61	0.11	-0.2732	2.7656
3 m	0.716 (0.636)	1.13	0.26	-0.5300	1.9611
6 m	3.040 (0.674)	4.51	<0.0001	1.7191	4.3616
10 m (bottom)	3.417 (0.597)	5.72	<0.0001	2.2467	4.5882

effect in question against the model without the effect in question. Where full models were significant, post hoc pairwise comparisons of significant terms were conducted using Tukey's HSD test, using the glht function in the multcomp package. Data were checked for conformity to assumptions of normality by visual examination of residual plots (lattice package) [42], and box cox transformations were used for non-normal residuals.

208 Additionally, we used the proportions of poor, average and high-quality larvae from each release site that settled to each 209 patch reef to create a connectivity matrix, and mapped down-210 stream connections to visually assess the influence of larval 211 phenotype on population connectivity. Lastly, we conducted a 212 targeted sensitivity analysis of our model (see electronic sup-213 plementary material 4(fo) full details), by varying 'target depth' 214 while holding all other model input parameters constant (i.e. aver-215 age-quality values), and applying the same statistical analyses 216 on the focused model outputs as described above. The purpose 217 of this analysis was to determine if phenotype-dependent effects 218 on dispersal outcomes still occur when the only difference 219 among phenotypes is the target depth that the larvae seek during dispersal. This 'target depth' parameter largely determines 220 their vertical depth distribution (vertical diffusion and currents can 221 also influence this). All statistical analyses were completed using 222 the statistical software R [30], and figures were created using the 223 package 'ggplot2' [43]. 224

3. Results

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(a) Vertical distribution patterns

230 Based on AICc criteria, the model of best fit for larval density 231 included the parameters depth, tide and time of day, but no 232 interactions terms (electronic supplementary mate للهزا); table 233 S2). This model suggests the pattern of larval distribution by 234 depth did not shift with either changes in tide or time, indicat-235 ing no diel vertical migration or selective tidal transport was 236 occurring. A higher abundance of T. caudimaculatus larvae 237 was caught during crepuscular periods and during flood 238 tides; however, these changes did not affect the relative depth 239 distribution of larvae (i.e. there was always a higher density 240 found in the bottom strata). Therefore, the model retaining 241 only depth as the best explanatory model was chosen, since 242 with no apparent vertical migration of T. caudimaculatus 243 larvae, the additional factors were not relevant to our ensuing 244 research questions. In comparing the selected model with the 245 null model, we found that larval density varied significantly 246 as a function of depth (table 1), with the majority (greater 247 than 90%) of T. caudimaculatus larvae found in the bottom two 248 strata (mean density \pm s.e.: surface = 5.1 \pm 2.4; 3 m = 6.9 \pm 2.4; 249 $6 \text{ m} = 73.3 \pm 41.0$; bottom = 128.0 ± 59.2 ; figure 1). Furthermore, 250 the depth distribution of T. caudimaculatus larvae did not vary 251 as a function of individual age (electronic supplementary material 3 (سنا S4). 252



Figure 1. Density of T. caudimaculatus larvae collected from depth stratified ichthyoplankton sampling. Densities were calculated as number of larvae per 100 m³ based on flow-meter determinations of the volume of water filtered Q12 per tow. Larger black circles represent the mean density at each depth.

(b) Quantifying Larval phenotypes

Phenotypic characteristics of larvae (size at hatch, early growth, instantaneous growth rate) varied among depth strata; larvae found in the surface stratum were smallest at hatch and grew slowest, and size at hatch and growth retenincreased with depth (electronic supplementary material ble S3). Based on otolith measurements, larvae collected from the surface stratum were on average 5% smaller at hatch than larvae found in the bottom stratum, and grew on average 15–20% slower than larvae at the bottom.

For statistical testing, and to account for non-independence, a composite variable of these three measures of larval phenotype was created using PCA. The first principal component (PC1) accounted for 66% of the overall variation in larval phenotype data. Size at hatch, early larval growth and instantaneous growth rate all loaded positively on PC1 (0.44, 0.62 and 0.64, respectively). Therefore, individuals with high PC1 scores were a larger size at hatch (indicative as greater development pre-hatching) and grew more quickly, relative to those with low PC1 scores.

Larval phenotype (as estimated by PC1) varied as a function of depth ($\chi^2 = 11.38$, d.f. = 3, p = 0.010) and this finding was not caused by bias in catchability of larvae due to depth or gear type (see electronic supplementary methods). Larvae found in the surface and 3 m strata were assigned negative PC1 scores (means: surface = -0.80 ± 0.19 ; $3 \text{ m} = -0.06 \pm$ 0.20), indicating that they hatched with small otoliths and grew at a slow rate, whereas larvae found in the bottom two strata were assigned more positive PC1 scores (means \pm s.e.:

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 Figure 2. PC1 score for larval quality of *T. caudimaculatus* larvae collected from depth stratified ichthyoplankton sampling. Positive PC1 scores indicate larvae that were larger at hatch and grew more quickly (i.e. high quality), whereas negative PC1 scores indicate larvae that were smaller at hatch and grew more slowly (i.e. poor quality). Larger black circles represent the mean PC1 score at each depth. Different letters represent significant differences determined by Tukey's HSD *post hoc* test.

 $6 \text{ m} = 0.16 \pm 0.14$; bottom = 0.18 ± 0.14), indicating that higher 277 quality T. caudimaculatus phenotypes were mostly found 278 deep in the water column (figure 2). Furthermore, the size of 279 T. caudimaculatus larvae at each day during the dispersal 280 period differed significantly among depth strata ($\chi^2 = 5497.1$, 281 d.f. = 31, p < 0.0001; see electronic supplementary material 3, 282 table S4 for parameter estimates and pairwise comparisons), 283 suggesting the growth trajectories of larvae at different 284 depths diverged shortly after hatch (electronic supplementary 285 material 3 ure S5). 286

(d) Modelled dispersal outcomes

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290 The biophysical model showed significant differences in three 291 of the four quantified measures of dispersal between low-, 292 average- and high-quality-hrval phenotypes (see electronic supplementary material able S5 for summary of model 293 294 output). Local retention and self-recruitment varied as a 295 function of larval phenotype (analysed alone, LR: $\chi^2 = 19.43$, 296 d.f. = 2, p < 0.001; SR: $\chi^2 = 16.53$, d.f. = 2, p < 0.001; analy-297 sed in migration matrix, LR: $\chi^2 = 25.46$, d.f. = 2, p < 0.001; SR: 298 $\chi^2 = 18.22$, d.f. = 2, p < 0.001). High-quality and average-quality 299 larvae exhibited a significantly higher proportion of local 300 retention (figure 3a) and self-recruitment (figure 3b) than 301 poor-quality larvae; on average, high-quality larvae were 302 more than twice as likely to recruit to their natal reef than 303 poor-quality larvae when analysed alone and within the inte-304 grated migration matrix. Mean relative geographical distance 305 travelled (GD) also differed among all three categories of 306 larvae ($\chi^2 = 54.02$, d.f. = 2, p < 0.001), with poor-quality larval 307 phenotypes travelling on average 49% further than average-308 quality, and 65% further than high-quality phenotypes 309 (figure 3c). As mortality was not included as a parameter in 310 the model due to the lack of direct empirical evidence, larvae 311 that were 'lost' represent individuals that were not successful 312 at finding suitable habitat before they reached their maximum 313 number of days spent in the plankton (50 days). No significant 314 differences existed in the proportion of larvae lost during the 315 pelagic dispersal period ($\chi^2 = 5.62$, d.f. = 2, p = 0.06; figure 3*d*); however, 56% more poor-quality larvae were lost compared to high-quality larvae.

Visual assessment of local population connectivity showed clear differences in the downstream connections resulting from the dispersal of poor-, average- and high-quality larval phenotypes (electronic supplementary material $\frac{3}{10}$ ure S6). Dispersal of poor-quality larvae resulted in a high number of connections between reef patches and low local retention, relative to average quality larvae. Dispersal of high-quality larvae resulted in even fewer downstream connections and the highest proportion of local retention. Overall, these main results were qualitatively similar to the targeted sensitivity analysis quantifying the influence of vertical distribution (through the 'target depth' parameter) on dispersal outcomes. The larvae's target depth during dispersal, and therefore the depth distribution, is clearly important in determining dispersal patterne and outcomes (see electronic supplementary material 4 full details).

4. Discussion

Many species on land and in water live in discrete habitat patches across highly fragmented landscapes, and dispersal is the key process responsible for connecting these local populations. The connections established by dispersing individuals have important consequences for local population demographics and persistence [3], to the extent where local population extinctions can be 'rescued' by recolonization of dispersers [1]. This study investigated how larval phenotype can influence dispersal and facilitate population connectivity in a temperate marine fish. The most striking finding from this study was that the position of individual larvae in the water column was strongly related to their phenotypic traits, with lower quality larvae found near the surface and higher quality larvae found near the ocean floor. This phenotypically structured vertical distribution of Trachinops caudimaculatus larvae suggests that individual phenotype (i.e. quality) can strongly influence the dispersal process, leading to fundamentally different dispersal outcomes. The results from our biophysical model support these predictions, and clearly illustrate how disperser phenotype can influence subsequent population connectivity in a marine metapopulation.

(a) Disperser phenotypes

Our study found evidence for the existence of dispersal syndromes within *T. caudimaculatus* larvae; larger, faster-growing larvae were found in the bottom two strata, whereas smaller, slower-growing larvae were found at the water surface. Furthermore, the growth trajectories of larvae at different depths show dispersal syndromes are strengthened throughout the dispersal period, as the size difference between individuals in the surface and bottom strate increased through time (electronic supplementary material 3 where so the strengthened to your biophysical model, this trait-dependent distribution of larvae through the water column creates distinct syndromes that correlate with dispersal distance—dispersers, the long-distance travellers found in the surface layers of the water column, and residents, the self-recruiters found in the bottom layers of the water column.

Theoretical and empirical studies suggest dispersal syndromes are a reflection of complex trade-offs and covariation among traits [10,44]. Often, traits that reduce the costs of

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Figure 3. Model estimates of four measures of dispersal outcomes: (a) local retention, (b) self-recruitment, (c) relative geographical distance travelled and (d) Q10 proportion of larvae lost in the dispersal period simulated for poor-, average- and high-quality larvae. Measures of local retention and self-recruitment shown 349 are from an integrated migration matrix, which accounts for the proportion of each larval phenotype in the cohort. Larger black circles represent mean values. 350 Different letters represent significant differences determined by Tukey's HSD post hoc test. Q12

354 movement (energetic, time, risk and opportunity costs) are 355 expected to covary with dispersal [5,44], however, dispersal syn-356 dromes or phenotypes may emerge as a response to a multitude 357 of ecological processes (e.g. competition, predation, reproduc-358 tion; [45]). While our study did not address the mechanistic 359 drivers of the vertical distribution of T. caudimaculatus larval 360 phenotypes, we can speculate on whether these disperser 361 types are a result of different adaptive behavioural strategies, 362 or the outcome of vertical positioning influenced by other 363 proximate causes.

364 The decision to move (horizontally or vertically) is gener-365 ally the result of balancing trade-offs between the costs 366 of migration and the potential benefits through reduced preda-367 tion risk, increased resource availability, and avoiding adverse 368 environmental conditions [46], and is dependent on both 369 extrinsic (e.g. population density, habitat cues, sex ratio and 370 social interactions; reviewed in [5] and [8]) and intrinsic (e.g. 371 body condition, sex, development and parental effects, and be-372 havioural phenotypes; reviewed in [47] and [24]) drivers. The 373 skewed distribution in density and the variability in larval 374 phenotype across depths found in this study are suggestive 375 of two possible strategies:

377 (1) Balancing of trade-offs between optimal depth and starvation/pre-378 dation risk. Since larval size and growth are known to be influenced by parental effects in a number of fish species (e.g. [48,49]), differences in larval phenotypes could represent within-population variability in offspring quality. The partial vertical displacement of the smaller individuals could reflect a behavioural decision to migrate upwards within the water column-maximizing current fitness through greater access to prey (either through higher prey availability or reduced competition with competitively superior individuals) or reduced exposure to potential predators, but a risky strategy for future fitness returns, as the dispersal pathway will incur greater costs [50].

(2) Balancing of trade-offs between dispersal and retention. Alternatively, the decision to disperse could be advantageous for an individual in a poor-quality environment, where the high costs of dispersing away from its natal habitat are balanced by potential future fitness gains, if higher-quality habitat is found at settlement. In contrast, individuals produced in a high-quality environment would benefit more from remaining close and recruiting back to their natal reef. As it is not known what population the T. caudimaculatus larvae sampled in our study came from, it is possible that the distinct disperser phenotypes in the water column represent among-population differences. For example, the 'retained' larval phenotype found in the bottom depth layers could have been released from

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379 Schnapper Point (the closest reef)-a high quality habitat 380 for T. caudimaculatus in PPB-and were recruiting back to 381 their natal reef, whereas the 'dispersing' larval phenotype at the surface could be dispersing from distant, lower qual-382 383 ity reefs in search of a better environment in which to settle. 384 While we cannot rule out this possibility, we would expect 385 that the 'disperser' phenotype would have fewer young larvae given the greater distances travelled, which was 386 387 not observed (electronic supplementary material gure 388 S4). Future research comparing the growth histories of 389 larvae dispersing long distances and those settling close 390 to or recruiting back to their natal reef is needed to test 391 this hypothesis.

It is also possible that the vertical distribution of larval 393 phenotypes is not indicative of a decision to move, but of differ-394 ential size-related abilities. A recent study by Nanninga & 395 Manica [51] found the swimming capacities of larval reef 396 fishes may be a powerful proxy for dispersal distance, evolution-397 ary connectivity and geographical range size in demersal marine 398 populations. As swimming performance typically develops 399 linearly with body size during larval ontogeny (e.g. [52,53]), a 400 fast-growing individual would develop a greater swimming 401 capacity than a slow-growing phenotype of the same age, with 402 greater capacity for self-recruitment by maintaining position 403 near reef habitat. Similarly, rapid development of swimming 404 capacity at an earlier age could be critical for a larva's ability to 405 control its vertical position in the water column, and could be 406 a proximate cause contributing to the heterogeneous distri-407 bution of larval phenotypes we observed in our study. 408 Determining whether either of these strategies is operating in 409 this system will require further research. 410

(b) Vertical positioning

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414 In assessing the vertical distribution patterns of T. caudimaculatus, 415 we found the highest densities of larvae were always in the two 416 deepest strata (6 m and 10 m), suggesting that T. caudimaculatus 417 are benthic-seeking larvae. This pattern of high densities with 418 depth was strong with respect to larval quality (figure 2), yet 419 did not vary as a function of the age of individual larvae, 420 suggesting an absence of ontogeny in vertical-distribution be-421 haviour. While vertical distribution and diel migration patterns 422 have been well documented in a number of important commer-423 cial and reef fish species (e.g. [54-56]), entirely benthic-seeking 424 larvae are relatively uncommon in the literature (e.g. [21]). This 425 heavily skewed vertical distribution in itself is an important find-426 ing, as implementation of the benthic seeking behaviour into a 427 dispersal model can have a significant influence on predicted 428 connectivity outcomes [35], particularly when larval quality 429 is considered as shown here. Despite a substantial focus on 430 the biological and physical drivers of dispersal over the past 431 two decades, empirical data on most aspects of larval dispersal 432 remain scarce (e.g. [57,58]). As a result, we increasingly rely on 433 models to estimate dispersal outcomes and demographic 434 connectivity [35,59]. However, due to a scarcity of supporting 435 empirical data, these models often lack aspects of larval behaviour that will lead to accurate predictions of dispersal and 436 437 connectivity estimates (reviewed in [60]). Our findings of atypi-438 cal larval behaviour further emphasize the importance of 439 collecting species-specific empirical data to support dispersal 440 models, and significantly improve the realism of modelled 441 connectivity estimates.

(c) Ecological implications of disperser syndromes

Our biophysical model simulations confirm our predictions that disperser phenotype can influence the number and strength of connections among local populations. Model simulations found low-quality larvae (small, slow-growth phenotypes) are transported further away from their natal reef, travelling greater distances, whereas high-quality larvae (larger, fast-growth phenotypes) remain near their natal reef and exhibit a higher proportion of self-recruitment and local retention. Not surprisingly, the poor-quality dispersers had a higher number of potential downstream connections than the average-or highquality larvae; however, they were also more likely to be 'lost' during the pelagic period, having failed to settle. These results illustrate an uneven distribution in the quality of successful dispersers across the dispersal kernel, with the poorest quality larvae travelling the greatest distance and driving the tail of the dispersal kernel. Although this pattern was consistent across the variable oceanographic conditions present in the year and location modelled in this study, further testing in other systems with different oceanographic conditions will be important for establishing the generality of this result.

Dispersal is a risky and costly endeavour [2,50], and longdistance dispersal often results in reduced larval fitness at settlement [19]. Furthermore, mounting evidence has shown that larval experience in the dispersal phase can significantly influence an individual's fitness and performance at the time of settlement [18,61] and in the post-settlement environment (e.g. [19]) through deferred costs of dispersal [50]. Given the quality of the phenotypes that our model predicted to disperse the greatest distances, the potential costs and compromises associated with dispersal, and the possible differential postsettlement survival linked to dispersal histories, it is likely that survival of these disperser phenotypes after settlement is low [50]. Such low survival can directly influence demographic connectivity [19], as 'realized connectivity'-the proportion of settled individuals from different larval sources that survive to reproduce—could potentially be much smaller than would be predicted without considering the influence of larval quality on dispersal pathways. This suggestion that local settlement should be more common among larvae of marine fishes is compatible with field evidence that suggests up to 60% of larval settlement is locally sourced [62] or settle close by [63,64].

Therefore, to more accurately predict connectivity and metapopulation dynamics, we must consider not just the proportion of immigration to each sub-population, but the relative *quality* of individuals arriving as well. Geographical distance between patches and/or hydrodynamic patterns in a system can result in particular patch reefs that receive primarily high-quality or primarily low-quality phenotypes (see electronic supplementary material 3 for ure S6), and this distinction in larval phenotype can be more important than variation in total larval supply in regulating metapopulation dynamics if, for example, a high-quality individual has a significantly greater capacity to survive and reproduce relative to a low-quality individual [65].

5. Conclusion

Interest in how individual variation influences dispersal outcomes has grown [8,47], however more work is needed to evaluate the role of individual traits (not mean traits) in driving population persistence and metapopulation structure and

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442 dynamics, particularly for marine ecosystems. Our research 443 illustrates the influence of disperser phenotypes on trajectories 444 and outcomes of dispersal, through simple vertical sorting of 445 larval phenotypes in the water column. Our findings highlight 446 the importance of appropriate sampling design (i.e. multiple 447 depth strata) to ensure the collection of accurate ichthyoplank-448 ton data. Furthermore, our biophysical model has shown that 449 phenotype-driven vertical distribution can lead to unique dis-450 persal outcomes due to larval quality, with low quality larvae 451 travelling the greatest distances, and can have implications 452 for population connectivity and metapopulation dynamics. 453 These differences may be compounded if larval quality is 454 found to impact other dispersal traits (e.g. buoyancy, homing 455 distance and larval mortality), and through differential fitness 456 and survival in subsequent life-stages associated with larval 457 quality. Failing to include measures of individual-based varia-458 bility in dispersal predictions may result in an overestimation 459 of population connectivity and metapopulation viability. The 460 hypothesis that larval phenotype could influence vertical dis-461 tribution and thus horizontal trajectories was first suggested 462 over four decades ago [23] yet there is surprisingly little empiri-463 cal evidence to support or refute our model. Given the 464 potential implications of our findings, and the relative ease of 465

collecting such data, more research should be conducted on other species and systems to test for the generality of our findings. As the dispersal stage is of fundamental importance to population persistence, continued empirical work aimed at understanding the ecology of dispersal is critical for effective conservation and management of spatially structured marine populations, particularly in the face of environmental change.

Ethics. All applicable institutional and national guidelines for the care and use of animals were followed in this study (University of Melbourne Animal Ethics Committee project ID: 1413189.1).

Data accessibility. The datasets supporting this article are available as electronic supplementary material.

Authors' contributions. E.K.F. and S.E.S. conceived and designed the study. E.K.F. performed the field sampling and otolith analysis. E.A.T. built the three-dimensional dispersal model and ran model simulations. E.K.F. analysed the data and wrote the manuscript. S.E.S. and E.A.T. edited the manuscript.

Competing interests. The authors declare that they have no conflict of interest.

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